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Heterochronic Quantitative Microevolution: Dental Divergence in Aboriginal Americans

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ABSTRACT Studies of tooth crown morphology alone have proven valuable in defining human population differentiation. We test the hypothesis that quantitative comparisons of more complex whole tooth structure may prove informative in understanding human diversity. Three disparate populations in Native American genetic history were compared: Kodiak Island Western Eskimos, Peruvian Inca Amerindians, and Southeast Asians. Enamel depth (an increasing gradient extended from Southeast Asians to the Inca) and root parameters were the most discriminating variables. The observed microevolution appears to result from variation in timing of known X-linked, Y-linked, and autosomal genes that affect either ameloblast or odontoblast differentiation. The dental traits were sexually dimorphic, the effect being more pronounced in aboriginal Americans, with male teeth having robust roots and thin enamel compared to female. Southeast Asians were isometrically related. The prominence of sexual dimorphism and the importance of sex-linked genes in the determination of the dental phenotypes suggest that sexual selection was one evolutionary force acting on early Asian populations. Subsequently, the selection appears to have been relaxed in Southeast Asians. Observed divergence of tooth shape among the populations, i.e., differences in the appropriation process of tooth primordia, was mainly the consequence of genetic drift modulating heterochronic regulators of homeotic genes.

Qualitative and quantitative investigations of tooth crown morphology alone have helped define phylogenetic relationships among human populations (Turner, 1984, 1990, 1992, 1994; Smith, 1994). We test the hypothesis that quantitative comparisons of more biologically and functionally complex whole tooth structure may prove powerful adjuncts to help discriminate among extant human populations, and may give clues to microevolutionary effects on dental characters. Three genetic culturally distinct Asian-based ethnic stocks were examined: Kodiak Island Western Eskimos, Peruvian Inca Amerindians, and Southeast Asians. These related populations were sampled because they have been temporally separated long enough for genetic drift to produce, at least theoretically, minor but not major quantifiable dental variation. If we are able to discriminate minor variation between at least two of these populations, then the employed methodology can meaningfully be applied to

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help dissect human evolution. Teeth are frequently critical aspects of finds of human remains. Since the crown is composed of nature's hardest material (enamel), teeth are more resistant to destruction with burial. The full exploitation of this rare resource, i.e., the quantification of all aspects of tooth structure, is important for the complete appreciation of dental variation among populations.

MATERIALS AND METHODS

Periapical X-rays were taken on a pre-European contact Kodiak Island, Western Eskimo sample (roughly at the time of first contact; 15♂/29♀; teeth = 94/318) derived from the Smithsonian Institution, Museum of Natural History, and an Ancón, Peru, Inca sample (pre-Inca Huari, ±600 A.D.; 18♂/9♀; teeth = 138/68) from the Field Museum of Natural History in Chicago. All mandibles were checked for the occlusal relationship with the maxillary complement and the fit of the condyles within the glenoid fossae. If incompatible, no films were taken. The sex of the material was first determined from the cranium and mandible (by E.D.S.) and then corroborated with museum sex data taken from the cranium, and postcrania if present. E.D.S. is the only individual to have seen all the museum material. If discordance occurred between E.D.S. and the Smithsonian Kodiak Island material, which was sexed at the time of collection, that material was excluded from the analysis. The Inca skeletal material was recently and very thoroughly documented and sexed by the Field Museum. Craniofacial sex determination of this material agreed with the museum assessment. The Southeast Asian sample (Chinese/Vietnamese) was derived from dental radiographs from inactive files at the dental clinic at the McGill University Faculty of Dentistry (17♂/23♀; teeth = 233/314). The same paralleling procedure for taking the periapical X-rays (see below) was utilized in the McGill Dental Clinic and in the museums, but E.D.S. did not take the dental clinic films. The use of dental films from this clinic has been proven reproducible (Shields et al., 1990). In order to accumulate large enough numbers, the Chinese and Vietnamese populations were combined. None of the individuals from the Chinese or Vietnamese samples were interviewed by the authors, only their records were examined. Country of origin was used as their identifier, no further information on origin was available. This sample a priori has a greater likelihood for large within-group variation.

Periapical radiographs of museum material were taken by a single investigator (E.D.S.) with a paralleling apparatus (XCP) that holds the film in a constant position parallel to the X-ray beam, thus reducing the potential for elongations and foreshortenings. Maxillary molars were not used since the lingual root makes interpretation very difficult. All other teeth were X-rayed unless wear extended through the dentino-enamel junction (DEJ), or the tooth was severely rotated and the film could not be placed parallel to its long axis. Southeast Asian teeth with large restorations were not measured. The tooth silhouettes were enlarged five times, tooth outlines drawn (by E.D.S.), including the pulp and the enamel extending up from the DEJ, and then the outlines digitized (by G.J.) for correction back to the original scale (Shields et al., 1990). The following tooth silhouette variables were quantified: 1) size measurement variables: tooth height (crown to apex: theight), tooth profile area (tarea), crown area (tcrown), root area (troot), maximal crown width (crown), root width at the midpoint between DEJ and apex (root), tooth width at the DEJ(DEJ), pulp profile area (parea) and relative pulp area (pratio = pulp area/tooth area), and enamel thickness, measured 1 mm from the DEJ (menamel = mesial and denamel = distal enamel depth); and 2) derived shape variables: crratio = crown area/root area and elongation = tooth width at the DEJ/tooth height.

Morphologic-functional and size-similar tooth elements were constructed for analysis of variance (ANOVA). For example, incisors are morphologically and functionally equivalent, nonetheless there is great disparity between the size of mandibular and maxillary incisors. Tooth size-similar elements were determined by Tukey's Studentized Range test, the elements being mandibular molars, maxillary incisors and all canines,

*TABLE 1. The ANOVA F value for each dental parameter among all ethnic stocks, the sexes, and ethnic stock * sex interaction (ethnic stock has two degrees of freedom, sex has one, and ethnic stock * sex has two)*[1]

Variable	Ethnic stock	Sex	Ethnic stock * sex
Denamel	77.1	39.5	1.8 ns
Menamel	89.2	31.9	4.9 ns
Tarea	23.5	47.6	2.0 ns
Tcrown	47.4	18.6	5.4 (.0048)
Troot	13.9	57.1	3.9 ns
Theight	9.1	18.5	0.5 ns
Dej	25.8	89.7	1.0 ns
Root	40.1	28.3	6.2 (.0021)
Crown	82.3	22.0	6.3 (.0019)
Crratio	22.3	3.1 ns	7.3 (.0007)
Elongation	61.1	11.9 (.0006)	3.3 ns
Pratio	30.6	0.1 ns	27.8

[1]The ethnic stock * sex interaction indicates significant differences in the degree of sexual dimorphism among the ethnic stocks. For all values $P < 0.0001$ unless given, or if the values were not significant (ns, $P > 0.005$).

premolars, and mandibular incisors. The ANOVA model included tooth elements, ethnic stock, sex, jaw and side as fixed effects, and individual museum number as a random effect. Only teeth with little wear were used in the analysis. Wear was a ranked variable that range from 0 (no attrition) to 6 (attrition extending close to the DEJ). Each tooth was assessed from the X-ray (by E.D.S.) for the relative loss of crown structure in relation to the DEJ (no measurement was done). So that crown area would not be compromised, only very mild wear of 0-2 was used. Moderate (wear = 3 or 4) and severe attrition are frequent findings that restrict the sample size for tooth area comparisons. Besides pulp area, all other root parameters are unaffected by attrition.

Symmetry was examined by comparing the signed difference in tooth areas (right-left, mm^2) between antimeres of each tooth element, their relative difference (R-L/overall tooth element mean), and Spearman rank correlation coefficient. Correlation was used to estimate the relation between tooth size and asymmetry, as suggested by Møller and Hoglund (1991).

RESULTS

Two-level ANOVA among the ethnic stocks, by sex, with ethnic stock * sex interaction (Table 1) showed highly significant differences among the ethnic stocks for all dental variables. To identify how the stocks related, we performed mixed-model ANOVA between each ethnic stock, by sex, for each dependent measurement variable (Table 2). Enamel depth in the cervical third of the crown was consistently informative for each ethnic stock and sex. A progression of increasing enamel depth occurred for both sexes, from the Southeast Asian (e.g., the distal enamel of all teeth combined, regardless of wear ([total sample] $♂\bar{X} = .55 \pm .19$ mm; $♀\bar{X} = .66 \pm .22$ mm), to Kodiak Island ($♂\bar{X} = .68 \pm .20$ mm; $♀\bar{X} = .74 \pm .22$ mm), to the Ancón sample ($♂\bar{X} = .78 \pm .24$ mm; $♀\bar{X} = .90 \pm .27$ mm). Variables that were informative for comparisons among the ethnic stocks (Southeast Asian males had small roots as compared to the other males, and the maxillary incisors and molars of all Southeast Asians had large crown areas), or sex comparisons (males had larger root areas), were chosen to illustrate graphically the relative relationship among the mean values of three key teeth (maxillary central incisors and canines, and mandibular second molars; Fig. 1). With the large numbers of tests done, all significance levels were set high ($P < .005$) to decrease the likelihood of accepting a false null hypothesis.

As shown in Table 1, sex differences among the samples were highly significant for most variables (crratio and pratio being the exceptions). The sex * ethnic stock interaction indicates differences in the degree of sexual dimorphism among the ethnic stocks. The degree of sexual dimorphism for each variable within each population sample is illustrated in Figure 2. Females had thicker enamel than males, while males had larger roots. Aboriginal Americans displayed an overall greater degree of sexual dimorphism than Southeast Asians. For Southeast Asians, the ratio of male to female values were similar for crown and root areas (overall Southeast Asian male/female scale: tcrown = 1.08, troot = 1.07). The sexes of aboriginal American populations differed in shape. Size and robustness of the root were the most important differences defining the Americans from the Southeast Asians, along with a decrease in crown size in Kodiak females. Kodiak Island females also had large relative pulp areas. The most striking dimorphisms in the Ancón sample were enamel

TABLE 2. The mixed-model ANOVA F value for each pairwise ethnic stock comparison (each dental parameter has one degree of freedom)

	SE Asian/West Eskimo		SE Asian/Inca		West Eskimo/Inca	
Variable	Male	Female	Male	Female	Male	Female
Denamel	10.0*	21.7*	120.6*	99.0*	38.3*	62.3*
Menamel	17.2*	83.5*	73.8*	136.9*	10.1*	39.4*
Tarea	3.5	11.3*	9.9*	0.1	18.8*	6.4
Tcrown	47.4*	66.1*	2.5	1.1	31.8*	40.4*
Troot	10.5*	0.8	32.5*	0.1	3.3	0.7
Theight	7.6	5.9	14.6*	14.1*	0.3	5.7
Dej	0.1	13.2*	30.7*	2.6	25.6*	0.1
Root	0.8	6.6	49.9*	3.1	27.2*	9.3*
Crown	0.7	41.2*	91.6*	75.1*	39.4*	36.6*
Crratio	43.4*	36.5*	33.3*	2.3	2.2	22.2*
Elongation	6.1	23.0*	112.2*	19.9*	34.2*	4.0
Pratio	16.1*	104.4*	53.4*	4.3	55.4*	15.9*

*$P < .005$.

depth and relative pulp area (males had large relative pulp space, opposite to that seen in the Kodiak sample). Maxillary incisors and all canines were the most dimorphic for size.

The complex segmental nature of teeth and their bilateral developmental distribution in both the maxillary and mandibular prominence of the first branchial arch, and the independent frontal nasal prominence, along with the protracted time for the full development of teeth, easily allow for potential environmental and genetic development perturbators to influence laterality. As shown in Table 3, neither left nor right was consistently larger in any stock (binomial tests for sign were not significant for either sex), and all teeth in each tooth element were symmetrical. Kruskal-Wallis tests (rank sums, to search for variation in symmetry) were not significantly different for either sex among the sample stocks. The variable "side" was not significant in any ANOVA.

As a descriptive summary of the association of the overall dental phenotype among the ethnic stocks, pairwise distances among males and females were calculated by canonical discriminant analysis (Fig. 3). Both derived variables and natural log transformed measurement variables were used in independent analyses of each tooth element irrespective of the variable's contribution to the separation among the elements. In spite of sample size restrictions imposed by a complete correlation matrix, multivariate statistics were highly significant for each tooth element (molars Wilks' Lambda = .23, $F_{(50, 546.1)} = 4.1$, $P < .0001$; maxillary incisors and canines $\Lambda = .35$, $F_{(50, 1453.7)} = 7.4$, $P < .0001$; premolars $\Lambda = .43$, $F_{(50, 1166.3)} = 4.8$, $P < .0001$; mandibular incisors $\Lambda = .23$, $F_{(50, 564.3)} = 4.3$, $P < .0001$).

DISCUSSION

ANOVA, along with plots of canonical discriminate analysis distances of the metric traits for each tooth element, showed that the population samples were easily separable, the sexes assorted by ethnic stock, and all populations were sexually dimorphic. The general impression of the overall dental phenotype given by the canonical plots is that the stocks are equally distanced. Within the global East Asian population, subsumed by all samples, enamel depth and root and crown sizes (especially the large size of Southeast Asian maxillary central incisors) effectively identified the independent ethnic stocks. Enamel depth and root size differences also typified the sexes. Sex differences in root size are, at least in part, a function of a growth-promoting Y-linked gene (Alvesalo and de la Chapelle, 1981; Alvesalo, 1985; Alvesalo et al., 1991; Garn et al., 1967) that in spite of being androgen independent, enhances male growth alone.

An incremental increase of enamel depth in both sexes extended from the thinnest in the Southeast Asian sample, to Western Eskimos, to the thickest in the Inca. Females had thicker enamel than males. In a study of dental X-rays utilizing the same methodology described here, significant sexual di-

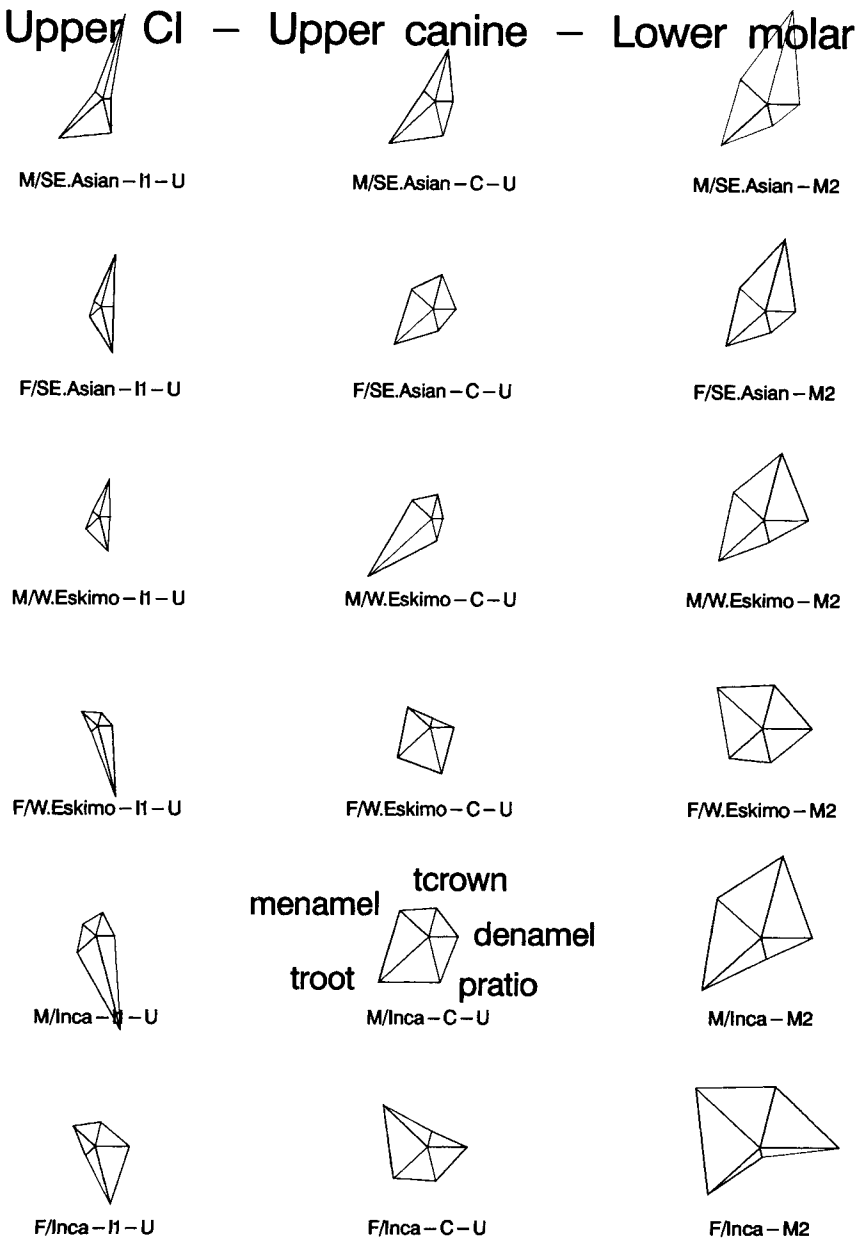

Fig. 1. Star plots of mean values of maxillary central incisor (Upper—CI), maxillary canine (Upper canine), and mandibular second molar (Lower molar), by sex (M and F), for each ethnic stock. The maxillary incisors, canines, and molars are represented as follows: I1-U = I^1; C-U = C^1; M2 = M_2.

morphism for enamel thickness, with females having thick enamel, was also found in present-day Western Europeans (E.D. Shields, unpublished observation). The likely biological basis for this sexual dimorphism is differential timing between the sexes of enamel matrix secretion. There are other examples of normal prolonged female development, for example, the timing of palatal shelf fusion is a week longer in human

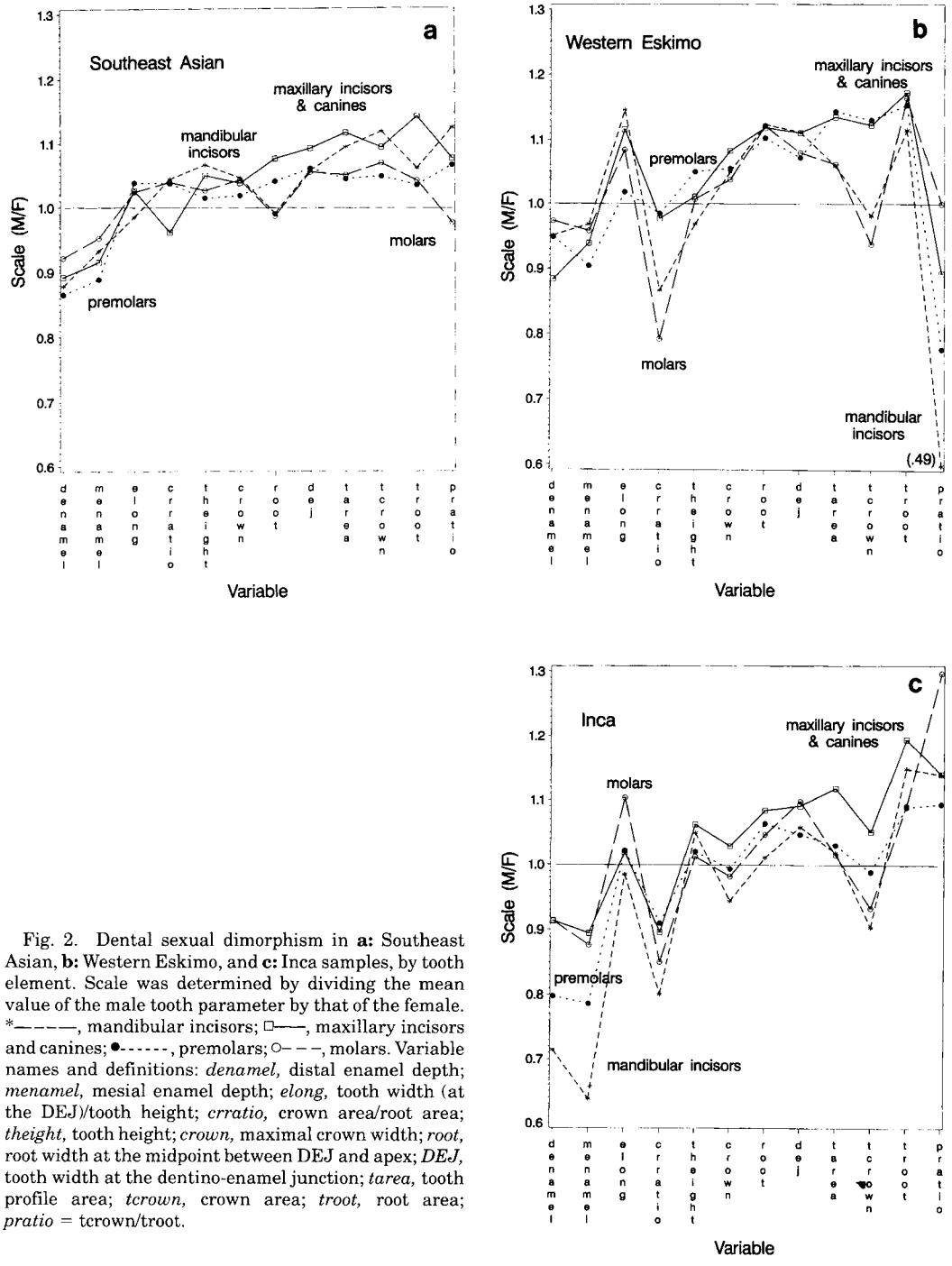

Fig. 2. Dental sexual dimorphism in **a:** Southeast Asian, **b:** Western Eskimo, and **c:** Inca samples, by tooth element. Scale was determined by dividing the mean value of the male tooth parameter by that of the female. *————, mandibular incisors; □——, maxillary incisors and canines; •------, premolars; ○– – –, molars. Variable names and definitions: *denamel,* distal enamel depth; *menamel,* mesial enamel depth; *elong,* tooth width (at the DEJ)/tooth height; *crratio,* crown area/root area; *theight,* tooth height; *crown,* maximal crown width; *root,* root width at the midpoint between DEJ and apex; *DEJ,* tooth width at the dentino-enamel junction; *tarea,* tooth profile area; *tcrown,* crown area; *troot,* root area; *pratio* = tcrown/troot.

female embryos (Burdi and Silvey, 1969). Alvesalo et al., (1987) have shown in X-chromosome aneuploidies that enamel depth, but not dentin depth, is directly correlated with the number of X-chromosomes. A gene was identified (AMEL) on both the X- and Y-chromosomes that codes for the major enamel matrix protein, amelogenin (Lau et al., 1989). Lagerström et al. (1990), using genetic-linkage analysis, identified that two X-

TABLE 3. Degree of asymmetry (difference) between antimeres and its sign for both sexes in each ethnic stock[1]

Population Tooth element	Sex	N	Signed[2]		Relative	r_s*
Southeast Asia						
Molars	M	9	−2.7	(4.4)	−0.017	0.22
Incisors and canines	M	24	4.3	(2.3)	0.031	−0.28
Premolars	M	24	0.1	(2.1)	0.001	0.18
Mandibular incisors	M	20	1.5	(1.6)	0.019	−0.14
Molars	F	10	−2.3	(3.8)	−0.015	0.12
Incisors and canines	F	46	−0.4	(1.2)	−0.003	−0.06
Premolars	F	27	0.4	(2.1)	0.004	−0.02
Mandibular incisors	F	25	−0.1	(1.2)	0.004	0.21
Western Eskimo						
Molars	M	2	−1.1	(10.7)	−0.007	·
Incisors and canines	M	10	1.3	(2.4)	0.01	0.07
Premolars	M	5	1.2	(1.6)	0.012	·
Mandibular incisors	M	5	−1.8	(1.1)	−0.022	·
Molars	F	17	−1	(2.1)	−0.007	0.03
Incisors and canines	F	39	−2.3	(1.2)	−0.02	0.21
Premolars	F	26	1.5	(0.9)	0.017	−0.12
Mandibular incisors	F	6	−1.6	(3.6)	−0.021	0.70
Peruvian Inca						
Molars	M	10	1.2	(2.9)	0.008	0.60
Incisors and canines	M	15	−1.2	(3.5)	−0.009	0.22
Premolars	M	9	1	(2.9)	0.01	0.02
Mandibular incisors	M	1	−2	(.)	−0.024	·
Molars	F	3	5.3	(9)	0.04	·
Incisors and canines	F	6	1	(5.6)	0.009	−0.26
Premolars	F	4	3.3	(3.9)	0.033	·
Mandibular incisors	F	4	−1.6	(1.9)	−0.02	·

[1] Tukey's Studentized Range test of tooth areas separated tooth elements into four groups of decreasing size, as ordered ($F_{(3)} = 600.2$; $P < .0001$). Kruskal-Wallis tests found no significant differences among the correlation coefficients for race or sex.
[2] Mean and s.e.
* Spearman rank correlation coefficient estimates the relation between asymmetry and absolute size (samples with less than six observations were not calculated). No correlation was significantly different from 0.

linked forms of amelogenesis imperfecta (AI) were linked to a single amelogenin gene. The Y-linked homologue has also been identified (Nakahori et al., 1991). There is extensive genetic heterogeneity among the numerous human nonsyndromic heritable defects of enamel formation (AI; Shields, 1983). The findings of homologous X- and Y-linked genes coding for a critical enamel protein (AMG), and that critical genetic variation exists, strongly suggest that pleiotropically induced variation at these loci are the basis for heterogeneity between the sexes and among the ethnic samples.

Variation in the extent and direction of sexual dimorphism, driven by root parameters and enamel depth, functioned as an independent trait complex that helped segregate the Southeast Asian sample from the North American stocks. Males had larger teeth. The Southeast Asian sample was the least dimorphic for shape and the moderate male tooth enlargement was isometric. Aboriginal American teeth were allometrically related due to robust male roots. Maxillary incisors and all canines were the most dimorphic for size. Western Eskimo females had large pulp chambers (thinner dentin as a result of an early termination of primary dentin matrix secretion, with no effect on secondary or tertiary dentin—Shields et al., 1990), a trend that was opposite to that of the other samples. The Inca sample was the most dimorphic for enamel depth.

Only a small amount of fluctuating asymmetry of tooth size was identified. Dividing the average tooth size (without regard to tooth element) by the average degree of asymmetry resulted in a 5.9% difference. This asymmetry is roughly compatible with crown dimension studies (Hershkovitz et al., 1993). The potential for error in tooth area from variation in bilateral tooth position/rotation should be greater than direct crown mesial/distal and buccal/lingual distance measurements. We thus presume that the actual asymmetry in the overall dental phenotype is smaller than observed. Consider-

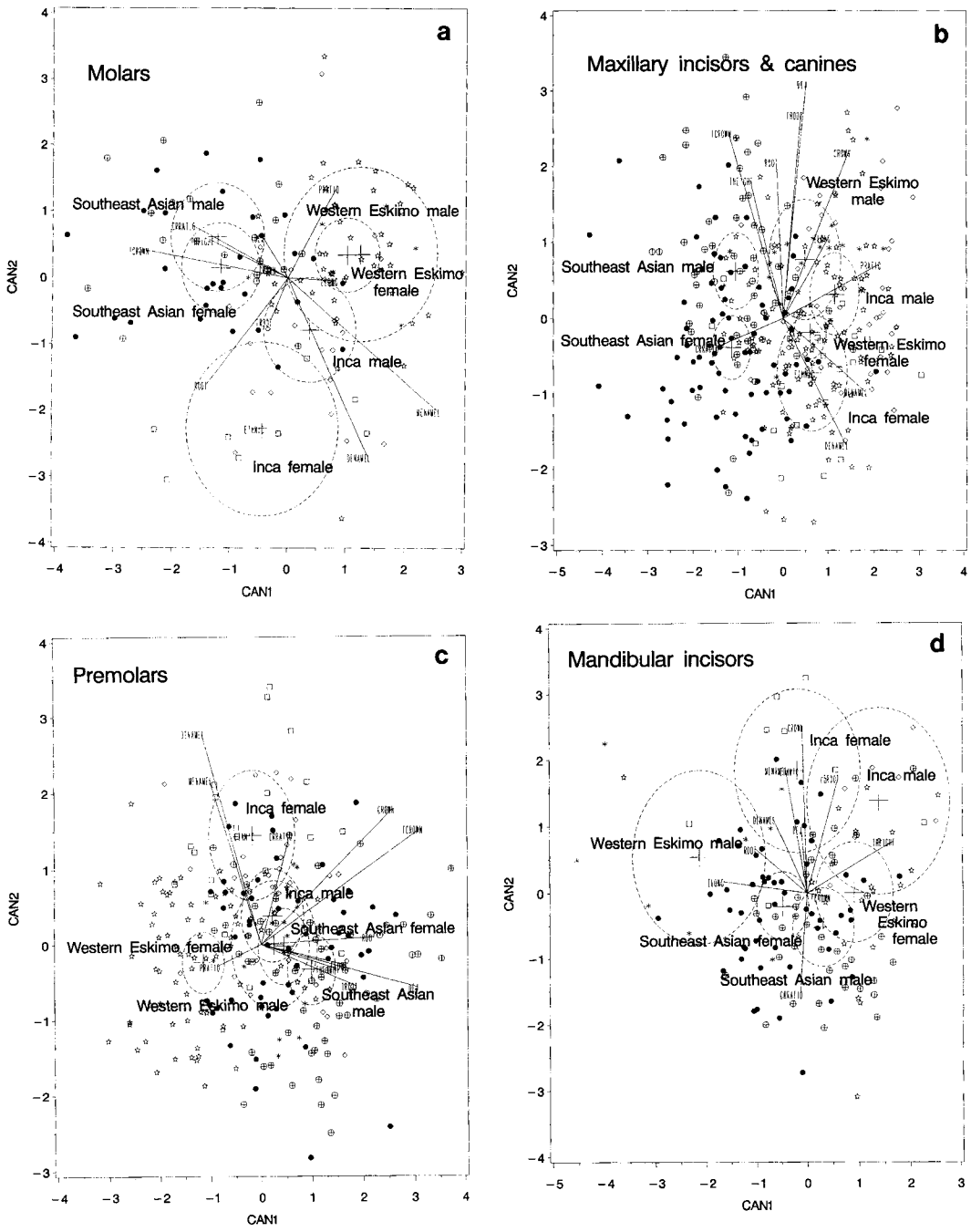

Fig. 3. Canonical discriminant analysis of the pairwise squared distances (Mahalanobis distances) among the ethnic samples for tooth elements: **a:** mandibular molars, **b:** maxillary incisors and canines, **c:** premolars, and **d:** mandibular incisors. Means (centroid = + for each "ETHNIC" or ethnic stock) and 99% confidence regions of the canonical variates are plotted. The canonical coefficient (correlation) scores of each variable are drawn as vectors of both canonical dimensions (CAN1 and CAN2). Vector length represents that variable's contribution to separation, its direction, and its relative contribution to that dimension (Kuhfeld et al., 1990). For the multivariate analyses, sample sizes were smaller since any missing value caused that observation to be deleted from the correlation matrix. Symbols represent as follow: ⊕ = Southeast Asian male; ● = Southeast Asian female; ◇ = Inca male; □ = Inca female; * = Western Eskimo male; ★ = Western Eskimo female.

ing the complexity of the morphogenesis of the overall dental phenotype, this small degree of natural variation is impressive. We appreciate the possibility of the presence of subtle asymmetry (Smith et al., 1982), and we will search for this when our sample sizes increase. Multifocal symmetry among all samples suggests that the initial neural crest-derived mesenchyme, which is induced for each tooth by the overlying oral ectoderm (Maina and Kollar, 1987), and thus constrained by it, has a strictly determined number of anlage, or primordial cells. It further suggests that tooth area is strongly buffered (canalized) against environmental variation since the environmental conditions under which the three samples existed were highly disparate.

Crown and root areas were both discriminating variables, nonetheless, overall tooth mass (tarea) was not an overly important factor among the stocks. This implies that same-sex differences in tooth shape among the sample populations were due to a differential appropriation of neural crest-derived ectomesenchyme to either the crown or the root, rather than differences in tooth anlage cell mass.

Homeobox genes (designated *Hox* in vertebrates) are evolutionary highly conserved genes that code for a family of homeodomain-containing protein transcription factors that help determine embryologic regional identity (periodic arrangements) along the anterior-posterior axis. Two known *msh*-like homeotic genes (*msh* is a *Drosophila melanogaster* muscle homeobox gene) function in the patterned initiation of mouse tooth crown (*Hox*-8 is temporally expressed in both the neural crest-derived mesenchyme that goes on to form the root, and the oral ectoderm that forms the enamel-MacKenzie et al., 1992) and root morphogenesis (*Hox*-7 is only expressed in root precursor mesenchyme-MacKenzie et al., 1991a, 1991b). Observed shape differences confirm MacKenzie et al. (1992) data that a major effect of the tooth-related homeotic genes is in the appropriation process, i.e., the determination of the outline of the basic tooth morphologic elements (e.g., incisors, molars). Homeotic genes thus likely modulate tooth shape by altering developmental timing. Tooth area comparisons between the sexes were significant. Sexual dimorphism in tooth area suggests that Y-linked growth-promoting genes increase the number of neural crest anlage cells. Retinoids (vitamin A and its metabolites) induce the expression of *Hox* genes and affect growth and differentiation (Pijnappel et al., 1993), and thus may be a determining factor of tooth area. Dental sexual dimorphism is effected much before male hormone (androgen)-related growth and the initiation of the oral ectoderm. The observed symmetry suggests that the determination of overall tooth size is a very early central effect (potentially an early embryonic midline diffusible signal such as retinoic acid) before neural crest migration (progenitor dental mesenchyme cells) to the branchial arches.

The microevolution described here was heterochronic (differences in developmental timing—Shea, 1989), probably involving controlling elements of gene expression that affect specific and independent stages of ameloblast and odontoblast differentiation. The length of time in the life history that both ameloblasts (enamel—Smith, 1979) and odontoblasts (primary dentin) spent secreting matrix (tissue depth), and the length of time of the inductive signal on Hertwig epithelial root sheath/odontoblasts (the number of cells within the root; i.e., root size), varied among the ethnic stocks and between the sexes. It can be argued that variance in enamel depth was a result of a differential speed of matrix production, especially among the stocks. We are unaware of studies that have addressed this issue in experimental animals. Although there have been several described human heritable enamel and dentin defects with abnormal timing of matrix production (Shields et al., 1973, 1990; Shields, 1983), we are unaware of any in which speed of matrix secretion was a parameter. Additionally, speed is a less biologically (and thus evolutionary) parsimonious site of alteration since speed of secretion is a more complex developmental process than the simple timing of matrix termination.

Natural selection of sex chromosome-linked traits is not the same as sexual selection, since sexual selection, among other things, may influence autosomal genes. Nonetheless, the observation that indepen-

dent and specific sex-linked aspects of cellular differentiation were sites of some of the heterochronic microevolutionary effects, and that sexual dimorphism was an important variable, suggests that sexual selection may have been an agent forcing early dental divergence in the progenitor Asian population. From the human perspective, the force of sexual selection can be very subtle. For example, it has recently been shown that the Y-linked sex-determining (testes) gene (*SRY;* Koopman et al., 1991) interacts with related transcription factor genes that influence such processes as bone development (Foster et al., 1994). A fevered mind could generate numerous hypotheses, some even testable, as to how sexual selection for one seemingly unrelated trait could then influence another. This putative selective force would have subsequently been relaxed in the Southeast Asian population. If megafauna extinction (Vantanyan et al., 1993) and rapid environmental change (Allen and Anderson, 1993; Alley et al., 1993; Levesque et al., 1993; Roberts et al., 1993) were factors prior to Paleoindian immigration, environmental directional selection may have been an additional evolutionary force in the potential small founder population from which both the Paleoindians and the Western Eskimos were eventually drawn. Genetic bottlenecks and rapid population expansion and dispersion were clearly important in the genetic history of aboriginal Americans. Thus, the likelihood is high that much of the observed evolution between the American samples was the result of random genetic drift.

We have shown that the quantification of whole teeth and comparisons of the degree of sexual dimorphism can be used meaningfully to complement other methods of morphometric taxonomy, especially tooth crown and individual dental trait investigations, by more fully exploiting a valuable resource. The methodology employed is a powerful means of identifying novel aspects of dental variation that are modulated by both selection and drift. We are presently extending this odontometric investigation to other extant human populations to clarify dental evolution, and hope to eventually include the major extant ethnic stocks and extinct hominids.

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